

A Revision of C. W. De Vis' Fossil Cormorants (Aves: Phalacrocoracidae)

WALTER E. BOLES

Ornithology Section, Research and Collections Branch,
Australian Museum, 6 College Street, Sydney NSW 2010, Australia
walter.boles@austmus.gov.au

ABSTRACT. C.W. De Vis named two species of fossil cormorant, *Phalacrocorax gregorii* and *P. vetustus*, from Pleistocene deposits at Cooper Creek and Warburton River, Australia, based on specimens mainly collected by J.W. Gregory in 1901–1902. The material of each nominal species consists of extensive, syntypic series of mixed elements. It was subsequently regarded that each series comprised specimens from several living species. One of these species, *P. fuscescens*, is an exclusively marine species, raising questions about its purported presence in central Australian deposits. Re-examination of the fossil material confirms that all specimens complete enough for identification can be referred to either of two living species, *P. carbo* or *P. varius*, or occasionally the Darter *Anhinga novaehollandiae*. There is no unequivocal evidence of the occurrence of *P. fuscescens*. Selections of lectotypes are made to synonymize *P. gregorii* with *P. carbo* and *P. vetustus* with *P. varius*.

BOLES, WALTER E., 2010. A revision of C. W. De Vis' fossil cormorants (Aves: Phalacrocoracidae). In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 145–155.

C.W. De Vis, of the Queensland Museum, named numerous fossil birds on the basis of specimens from the Darling Downs, southeastern Queensland, and the Cooper Creek/Warburton River region of South Australia (De Vis, 1888a,b, 1889, 1892, 1905). Although he was prolific, De Vis lacked more than a cursory reference collection, missing representatives of a number of the families to which he allocated taxa. He also held the belief that fossils could be related to, but had to be separate species from, living ones. Many of his taxa are still recognised, but a number of species have been found to be allocated to the wrong family, or to be junior synonyms of living species, or both (summarized by van Tets & Rich, 1990).

Most of his nominal species have been reviewed (megapodes: van Tets, 1974; ducks: Olson, 1977; pelicans: Rich & van Tets, 1981; storks: Boles, 2005; flamingos: Rich *et al.*, 1987; birds of prey: Rich *et al.*, 1982, Gaff, 2002; rails: Olson, 1975; pigeons: van Tets & Rich, 1980). Among the few that await detailed re-examination are the cormorants.

De Vis (1905) erected two species from central Australian material, *Phalacrocorax gregorii* and *P. vetustus*, each on the basis of large syntypic series of assorted skeletal elements (Tables 1–8). He gave few details on the characters used to diagnose these species. Lambrecht (1933) created the genus *Australocorax* for them (type species *Phalacrocorax gregorii*). cursory examination of the material led G.F. van Tets (pers. comm. in Condon, 1975) to suggest possible synonymy with the Pied Cormorant *Phalacrocorax varius*. Later, Rich & van Tets (1982), van Tets (1984) and van Tets & Rich (1990) considered that De Vis' series comprised composites of modern forms, the Pied Cormorant, Great Cormorant *P. carbo* and Black-faced Shag *P. fuscescens* (sometimes placed in the genus *Leucocarbo*) and, in the case of *vetustus*, the Darter *Anhinga novaehollandiae*, as well. Rich & van Tets (1982) provided a list of De Vis' fossil bird specimens, with an indication of proposed identifications. Each of the cormorant bones was tentatively associated with a living species. No indication was given in that list regarding

the basis on which the specimens were attributed to which taxa, and, although reference is made to “van Tets & Rich, in prep”, this has not been published subsequently.

Owing to van Tets’ longstanding interest in cormorants, both fossil and living, it is very likely that he was responsible for most, if not all, of these specific allocations. Annotated labels accompanying specimens in the Queensland Museum collection cite his identifications. In addition, an unpublished manuscript by van Tets in the Australian National Wildlife Collection, Canberra, gives some insight into his thinking, although it does not provide the characters for his species identification. He noted that De Vis’ reference collection apparently contained only *P. carbo* and Little Black Cormorant *P. sulcirostris* (which appears to have had significant ramifications in the descriptions of *gregorii* and *vetustus*). This manuscript was consulted during this study, but a number of the conclusions differ.

One of the most interesting, and controversial, aspects of van Tets’ identifications is the allocation of some specimens to *P. fuscescens*, an exclusively marine species (Marchant & Higgins, 1990). Its presence in central Australia would be unexpected, but if valid, could have resulted from an isolated population associated with a marine incursion into this low lying region. Alternatively, according to Rich & van Tets (1982), “It appears that there may have been a land-locked population of a *Leucocarbo* similar to the Black-faced Shag in the Lake Eyre Basin during the Pleistocene, analogous to that of the almost land-locked European Shag, *Stictocarbo aristotelis* in the Mediterranean, and an extinct, small gannet, *Morus*, in the Black Sea”.

The aims of this study are (a) to identify and allocate these bones to the correct species, where possible, and, (b) if there are no unnamed fossil forms represented, synonymize De Vis’ cormorants with living ones by designating a lectotype for each.

Geology and geographic setting. Almost all of the specimens considered here were collected on J.W. Gregory’s 1901–1902 trip to central Australia, along the Cooper Creek and Warburton River, northeastern South Australia (Gregory, 1906; Fig. 1). Specific site names were cited by De Vis (1905) for many of the specimens, but others have no more general location than “Lower Cooper Creek”. Tedford & Wells (1990) were able to locate many of Gregory’s place names,

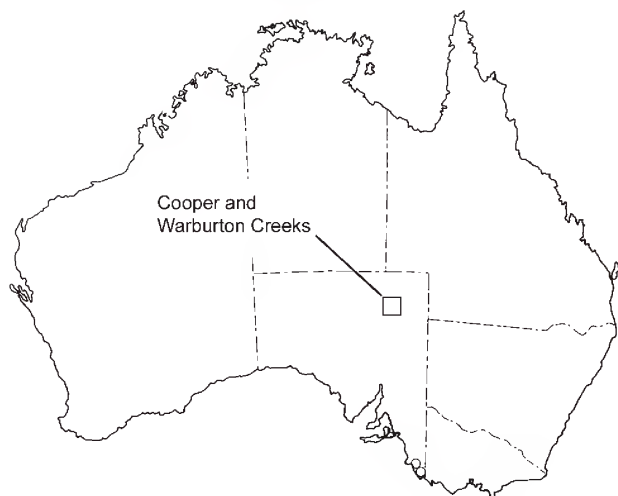


Figure 1. Location of portions of Cooper and Warburton Creeks, South Australia, relevant to this study.

but others could not be found on his map, so their precise localities could not be confirmed. Various, but phonetically similar, spellings were used for several sites by Gregory (see discussion in Tedford & Wells, 1990) and apparently repeated by De Vis in his descriptions. Malkuni (or Malkuni Waterhole; also Mulcani), also known as Emu Camp, is a well established locality along the Cooper. Wurdulmankula (also written as Wurdumankula and Wurdumulankula) and Wankameminna, as well as those given only as Lower Cooper, could not be determined by Tedford & Wells (1990). The Kalamurina locality of Gregory is near the old Kalamurina Homestead along the Warburton River.

A maxilla described by De Vis was collected by the Government Geologist, H.Y.L. Brown. De Vis cited the locality as “(?)”, whereas Rich & van Tets (1982) gave it as Cutupirra (= Katipiri = Kutipirra) on Cooper Creek. Brown’s collections, however, were made on a stretch of the Warburton River, including the Kalamurina area (Brown, 1892).

Tedford & Wells (1990) recognized that the fossil material from these Cooper Creek sites represented two faunas: the Malkuni Fauna from the Katipiri Formation and the slightly older Lower Cooper Creek Fauna from the Kutjitara Formation, while those at the Warburton River were part of the Kalamurina Fauna; all represent primarily fluvialite accumulations. The fossils considered in this paper come from the Middle to Late Pleistocene Katipiri Formation. This comprises mostly unconsolidated, fine white sand, with interspersed mud drapes accumulated during several episodes of deposition. The deposits overlie or are partly incised into the older Tirari and Kutjitara Formations.

Many specimens of the Malkuni Fauna were found as “float” on sandbars or river bed in the watercourse, while others occurred at the base of cliff in which the Katipiri Formation is exposed. The mammalian fauna was a mixture of now extinct taxa, such as diprotodontids, and living forms, such as koalas *Phascolarctos* and Agile Wallabies *Macropus agilis* found today in eastern and northern parts of the continent, respectively. For more detailed discussion of the geology and faunas of this region, see Stirton *et al.* (1961), Lundelius (1983), Woodburne *et al.* (1985), Tedford *et al.* (1986); Tedford & Wells (1990); Nanson *et al.* (2008); and references therein.

Materials and methods

The De Vis specimens are housed in the Queensland Museum, with the exception of P18413 (premaxillary) held in the South Australian Museum. Morphological characters were taken from Owre (1967), Ono (1980), Gilbert *et al.* (1981) and Siegel-Causey (1988) and from direct comparisons of specimens. Institutional prefixes to registration numbers of comparative material used in this study are AM (Australian Museum), ANWC (Australian National Wildlife Collection), MV (Museum Victoria) and SAM (South Australian Museum). Terminology of bones largely follows Baumel & Witmer (1993). Measurements follow the methods illustrated by Steadman (1980) and were made with digital calipers accurate to 0.01 mm and rounded to the nearest 0.1 mm. A number of De Vis’ specimens are broken, thus often rendering the comparative measurements inapplicable, requiring direct comparisons with reference skeletons by eye. Scientific names of Australian species follow Christidis & Boles (2008).

Systematic paleontology

Also described from Cooper Creek is the fossil darter *Plotus laticeps* De Vis, 1905. This was subsequently synonymized with the extant *Anhinga novaehollandiae* (Mackness & van Tets, 1995). Cormorants and darters are similar osteologically, but exhibit consistent differences in major elements so that separation is possible for sufficiently intact bones. Differentiating the species of cormorants found in Australia is more reliant on size than morphological features in these quite osteologically uniform birds. The size sequence, from largest to smallest, is *Phalacrocorax carbo*, *varius*, *fuscescens*, *sulcirostris* and *Microcarbo melanoleucos* (Little Pied Cormorant); the last two are markedly smaller-bodied birds than *P. gregorii* and *P. vetustus* and are not of further concern here. Other than *melanoleucos*, Australian cormorants are dimorphic in size, with males being the larger sex. There is usually a small to moderate degree of overlap in size between the female of the larger species and the male of the next species in the sequence; for example, see Fig. 2, which illustrates these relative sizes for the proximal femur. Other features, such as comparative robustness of the bones, are useful for specimens in this range of overlap.

In the following consideration and re-evaluation of the specimens, a few characters for the separation of *Anhinga* and *Phalacrocorax* are presented first, followed by criteria for distinguishing the species of cormorants; these are characters sufficient to separate taxa, but are not exhaustive. In almost all cases where there is a potential question about the identity of a specimen, it is one between *carbo* and *varius* or *varius* and *fuscescens*. Finally, the determinations of the fossils from this study are given, with discussion of those that disagree with the assignments in Rich & van Tets (1982).

Premaxillary. SAM P18413, the only specimen held other than at the Queensland Museum, consists of an entire maxilla from the tip to the nasofrontal hinge. It is easily identified as that of a cormorant rather than of a darter by having the tip hooked, rather than straight and pointed. De Vis cited the locality as “(?)”, whereas Rich & van Tets (1982) give it as Cutupirra on Cooper Creek. De Vis stated that it most closely resembled *P. carbo* and, indeed, “its non-identity with the living cormorant of southern waters depends on that or the numerous bones associated with it”. Rich & van Tets (1982) gave the identification as *varius*.

The specimen is 78.5 mm from the tip to the nasofrontal hinge; the width at the hinge is 15.9 mm. The length falls in the overlap zone between *carbo* and *varius*. The latter, however, is proportionally thinner (13.5–16.4 mm) than *carbo* (16.7–17.5 mm). The maxilla of *gregorii* is within the range

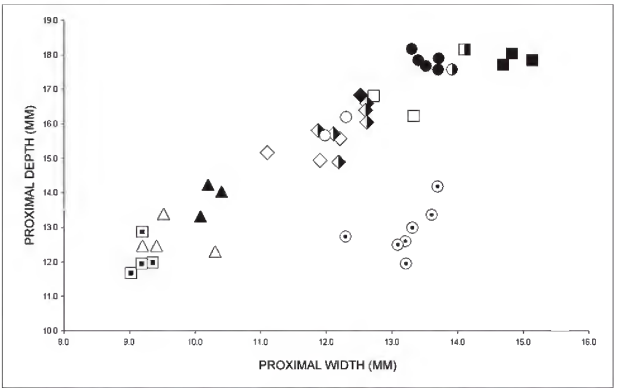


Figure 2. Measurements of the proximal end of the femur for extant Australian species of cormorant *Phalacrocorax* illustrating sexual size dimorphism within species and overlap between species. Species: squares, *Phalacrocorax carbo*; circles, *P. varius*; diamonds, *P. fuscescens*; triangles, *P. sulcirostris*; square with dot, *P. melanoleucos*; circle with dot, *Anhinga novaehollandiae*. Sex: males, black; females, white; unsexed, half and half.

of *varius* and is here considered to belong to that species, confirming the identification by Rich & van Tets (1982).

Coracoid (Table 1). *Phalacrocorax* is separated from *Anhinga* by having the facies articularis sternalis strongly lipped on the ventral surface. *Phalacrocorax carbo* and *varius* differ mainly in size, rather than morphology, with some overlap between females of the former and males of the latter. *Phalacrocorax varius* differs from *fuscescens* by having the sternal end of the facies articularis humeralis wider (Fig. 3).

gregorii—De Vis assigned two coracoidal specimens to this species. Most of his description was devoted to a fragment of the humeral end (F3755). Although it was “about the same size as in *P. carbo*”, De Vis remarked that it “conspicuously differs in the size and form of the facets for the humerus and, particularly, the scapula, which is a deep cup-shaped cavity, occupying the entire articular surface of the procoracoid process”. These and other characters presented are unlike *carbo* for a good reason: this bone (F3755) is, in fact, from a heron (Ardeidae), as was recognized by Rich & van Tets (1982). This identification was confirmed, the Ardeidae being separated from the Phalacrocoracidae and Anhingidae by the combination of having the processus procoracoideus triangular (small rounded bump in Phalacrocoracidae and Anhingidae), cotyla scapularis round and deep (obsolete), impressio lig. acrocoracoideum wide and rectangular (narrow, extending far sternally), sulcus m. supracoracoideus very broad, not bounded by ridges on sides, bordered

Table 1. Coracoids of De Vis’ cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end, *c*, complete; *h*, humeral; *st*, sternal; side: *l*, left; *r*, right.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
<i>Phalacrocorax gregorii</i>					
F3754	st	r	Lower Cooper	<i>carbo</i>	<i>carbo</i>
F3755	h	r	Wankameminna	Ardeidae	Ardeidae (large)
<i>Phalacrocorax vetustus</i>					
F3789	p	r	Malkuni	<i>carbo</i>	<i>varius</i>
F3790	h	r	Malkuni	<i>fuscescens</i>	<i>varius</i>
F3791	st	l	Kalamurina	<i>fuscescens</i>	<i>varius</i>



Figure 3. Shoulder end of coracoid (dorsolateral view) showing differences in the width of the sternal end of facies articularis humeralis between (A) *Phalacrocorax varius* and (B) *P. fuscescens*.

humeraly by the more or less flat edge of facies articularis clavicularis (narrow and elongate, bounded on sides, pointed humeraly). F3755 comes from a large heron. In his unpublished manuscript, van Tets referred it to the Large-billed Heron *Ardea sumatrana*, Australia’s largest bodied heron. The size of this fossil is comparable to the Great Blue Heron *A. herodias* of the New World (Fig. 4). A taxonomic allocation of this specimen to *A. sumatrana* raises more questions than those arising from the putative presence of *P. fuscescens*. *Ardea sumatrana* occurs along the coasts of northern Australia, New Guinea and western Indonesian islands, where it is almost exclusively a bird of mangroves.

vetustus—Regarding the coracoid of this species, De Vis remarked, “The unlikeness of this to the coracoid of *P. gregorii* is great”. Again, because of the misidentification of the latter, this is not surprising. Of the three specimens, Rich & van Tets (1982) listed one as *carbo* and the other two as



Figure 5. Proximal end of humerus (cranial view) showing differences in distal delimitation of the impressio coracobrachialis in (A) *Phalacrocorax fuscescens* and (B) *P. varius*.

fuscescens. Re-examination indicates that all can be referred to *varius*. The size of F3789 is more indicative of this species than *carbo* and the other two specimens are distinguished from *fuscescens* by the characters given above.

Humerus (Table 2). Cormorants differ from darters by having the fossa pneumotricipitalis deeper proximally, tuberculum dorsale forming a sharp angle (rather than rounded) and impressio coracobrachialis proportionally narrower (in *Anhinga*, this comprises 50% or more of cranial face of the proximal end). Rich & van Tets (1982) did not refer any humeral specimens to *Anhinga*.

Size is a good distinguishing character for some species, with male *carbo* being detectably larger than other taxa. For the two smaller species, *fuscescens* can be separated

Table 2. Humeri of De Vis’ cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *p*, proximal; *s*, shaft; *d*, distal; side: *l*, left; *r*, right.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
<i>Phalacrocorax gregorii</i>					
F3756	p	l	Malkuni	<i>carbo</i>	<i>carbo</i>
F3757	d+s	r	Kalamurina	<i>carbo</i>	<i>carbo</i>
F3758	d+s	r	Lower Cooper	<i>carbo</i>	<i>carbo</i>
F3759	d	r	Lower Cooper	<i>carbo</i>	<i>carbo</i>
F3760	s	r	Malkuni	<i>carbo</i>	<i>carbo</i>
F3761	d	l	Malkuni	<i>carbo</i>	<i>carbo</i>
F3762	d	l	Lower Cooper	<i>carbo</i>	<i>varius</i>
<i>Phalacrocorax vetustus</i>					
F3792	p	l	Malkuni	<i>fuscescens</i>	<i>varius</i>
F3793	p	l	Malkuni	<i>fuscescens</i>	<i>varius</i>
F3794	p	l	Malkuni	<i>fuscescens</i>	<i>varius</i>
F3795	d	l	Kalamurina	<i>fuscescens</i>	<i>varius</i>
F3796	d	l	Malkuni	<i>varius</i>	<i>varius</i>
F3797	d	r	Lower Cooper	<i>carbo</i>	cf. <i>carbo</i>

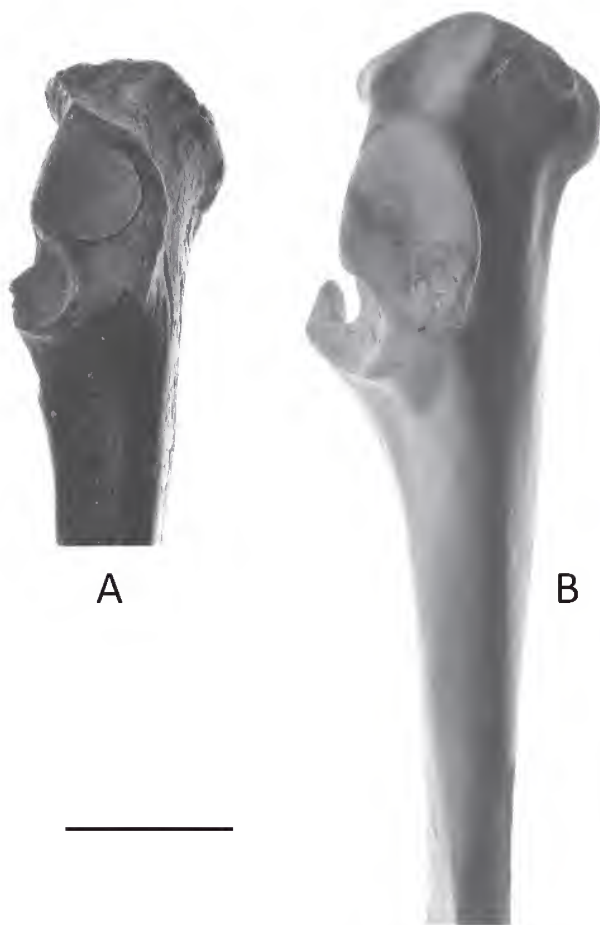


Figure 4. Shoulder end of coracoid (dorsal view) showing similarities in morphology and size between (A) QM3755 and (B) *Ardea herodias*.

from *varius* by the depth and distal extent of the impressio coracobrachialis (Fig. 5). In *fuscescens* it is deep and terminates abruptly with a marked distal border, whereas in *varius* the impressio is shallower with the distal border low and merging more smoothly into the shaft. The distal end of *varius* differs from those of both *carbo* and *fuscescens* by having the fossa m. brachialis more excavated, particularly on the ventral side such that its border is much more prominent (Fig. 6).

gregorii—All the specimens except F3762 can be identified as *carbo* based on size and morphology. F3762 is referred to *varius*, rather than *carbo*, by the structure of the fossa m. brachialis (see above).

vetustus—Three proximal fragments of *vetustus* (F3792–4) were considered by Rich & van Tets (1982) to belong to *fuscescens*. They are here placed with *varius* on the condition of the impressio coracobrachialis. A distal fragment (F3795) was also considered to be *fuscescens* by Rich & van Tets

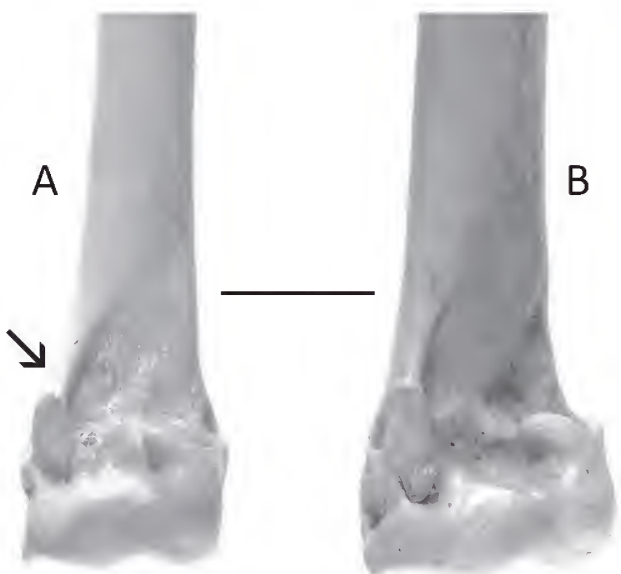


Figure 6. Distal end of humerus (cranial view) showing differences in excavation of the fossa m. brachialis in (A) *Phalacrocorax varius* and (B) *P. carbo*.

(1982) but exhibits the deeper fossa m. brachialis of *varius*. A specimen of a young bird not fully ossified (F3797) retains a portion of shaft that is slightly more robust than in *varius* and shows less curvature; its reidentification by Rich & van Tets (1982) as *carbo* is tentatively confirmed. Another specimen, a right distal fragment from Kalamurina assigned to *vetustus*, was lost subsequent to the description by De Vis (1905) and thus not registered in the Queensland Museum collection.

Ulna (Table 3). The proximal end of the cormorant ulna differs from that of the darter's by having the cotyla dorsalis broader (proximal view) and the processus cotylaris dorsalis with a prominent triangular, dorsodistally directed projection.

The character states listed by Siegel-Causey (1988) indicated that the attachment of *M. bicipitis* connects the depressio m. brachialis by a strong ridge in *varius* but these are separate in *fuscescens*; this could not be confirmed. Characters of the proximal end by which these species can be separated are, in *varius*, the proximal end of the depressio m. brachialis is deeper, extending further proximally and undercutting the tuberculum lig. collateralis ventralis; in *fuscescens*, the sulcus tendineus is deeper throughout its extent with more sharply defined borders and the tuberculum lig. collateralis ventralis projects further cranially. Compared to that of *varius*, the ulna of *carbo* is more robust, on the proximal end notably in the development of the olecranon.

vetustus—De Vis referred no ulnar specimens to *gregorii* but placed two proximal fragments with *vetustus*. Unfortunately, damage to the both specimens prevents any of the preceding

Table 3. Ulnae of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: p, proximal; side: r, right.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
<i>Phalacrocorax vetustus</i>					
F3798	p	r	Malkuni	<i>fuscescens</i>	cf. <i>varius</i>
F3799	p	r	Wurdumankula	<i>fuscescens</i>	cf. <i>varius</i>

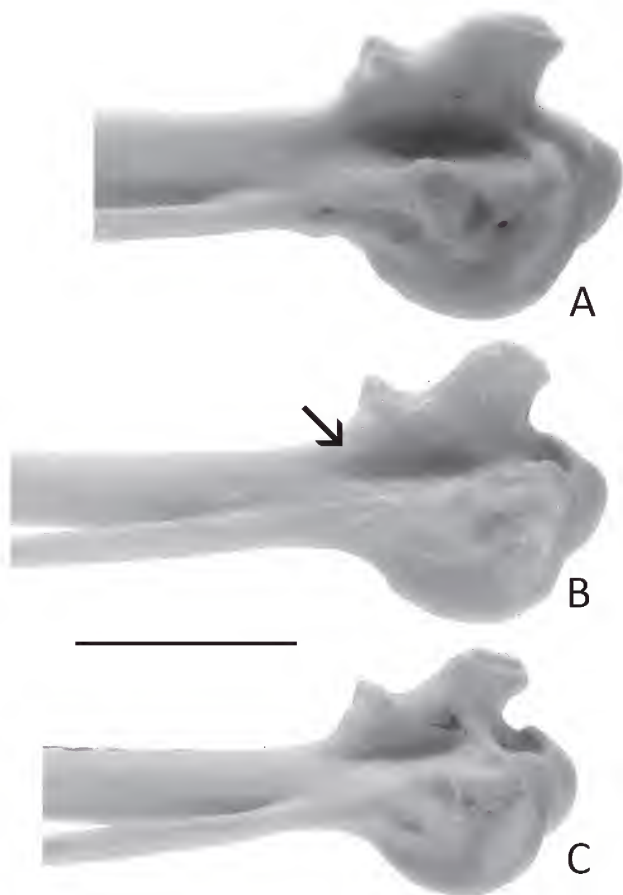


Figure 7. Proximal end of the ventral side of the carpometacarpus (ventral view) showing differences in excavation for the insertion of *M. flexor digiti II* in (A) *Phalacrocorax carbo*, (B) *P. varius* and (C) *P. fuscescens*.

characters being assessed with confidence. What structures remain, however, show greater resemblance to the conditions in *varius*, and these specimens are tentatively referred to that species.

Carpometacarpus (Table 4). In *Phalacrocorax*, the processus pisiformis is situated at the centre of the ventral side of the trochlea carpalis, whereas in *Anhinga* it is distal to this midpoint. Cormorants also have a deeply incised fovea carpalis cranialis, whereas this feature is absent in *Anhinga*.

Cormorants have an excavation on the ventral side of the proximal cranial to the processus pisiformis for the insertion

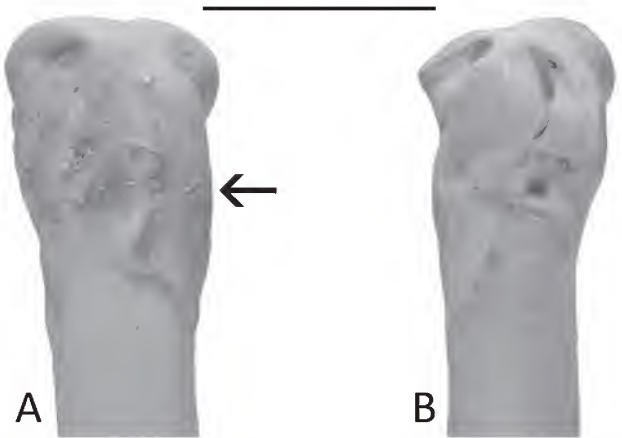


Figure 8. Proximal end of femur (lateral view) showing differences in development of the cranial border of the facies articularis antitrochantericus between (A) *Phalacrocorax* and (B) *Anhinga*.

of *M. flexor digiti II*. In addition to its larger size, *carbo* can be recognized by having this excavation deeper (Fig. 7B). In *fuscescens*, this excavation extends cranially into the base of the processus extensorius (Fig. 7A). Compare these states with that of *varius* (Fig. 7C) in which the excavation is shallower and lacks the cranial extension.

gregorii—Both specimens, placed with *carbo* by Rich & van Tets (1982), agree with that species in size and morphology.

vetustus—Although F3800 falls into an area of overlap in size between *fuscescens* and *varius*, the structure of the insertion of *M. flexor digiti II* and the overall robustness indicate that it represents the latter species. The distal fragment F3801 is on size either a female *carbo* or male *varius*; an assignment cannot be made with confidence. F3802, a proximal end, is also intermediate in size between these species; abrasion to the ventral side prevents positive assessment of the degree of excavation but it appears to be more similar to *varius*.

Femur (Table 5). Cormorants have the craniocaudal expansion of the lateral side of the proximal end, notably that caused by the cranially expanded crista trochanterica femoris, very obvious in lateral view (Fig. 8), and the cranial border of the facies articularis antitrochanterica is well pronounced, delimiting the proximal end from the cranial face of the shaft (Fig. 9). In *Anhinga*, there is little expansion of the crista trochanterica femoris nor is the facies articularis antitrochanterica strongly bordered on its cranial side. On

Table 4. Carpometacarpi of De Vis’ cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *c*, complete; *p*, proximal; *d*, distal; side: *l*, left; *r*, right; sex: *M*, male; *F*, female.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
<i>Phalacrocorax gregorii</i>					
F3763	c	r	Lower Cooper	<i>carbo</i>	<i>carbo</i>
F7020	p	r	Malkuni	<i>carbo</i>	<i>carbo</i>
<i>Phalacrocorax vetustus</i>					
F3800	p	r	Wurdumankula	<i>fuscescens</i>	<i>varius</i>
F3801	d	l	Lower Cooper	<i>carbo</i>	<i>carbo</i> F / <i>varius</i> M
F3802	p	l	Malkuni	<i>carbo</i>	cf. <i>varius</i>
F3803	c	r	Lower Cooper	<i>varius</i>	<i>varius</i>



Figure 9. Proximal end of femur (cranial view) showing differences in extent of craniocaudal expansion of the trochanteric region between (A) *Phalacrocorax* and (B) *Anhinga*.

the distal end (Fig. 10), the trochlea fibularis is more robustly developed in *Phalacrocorax* and the attachment for *M. flexor hallicus longus* is expressed as a deep depression lateral and proximal to the condylus lateralis and proximal to the trochlea fibularis (depression small or absent in *Anhinga*).

The only apparent differences among the species of cormorants are ones of size.

gregorii—Rich & van Tets (1982) assigned specimen F3767 to *Anhinga laticeps* (De Vis, 1905) (now synonymized with the living *Anhinga novaehollandiae*: Mackness & van Tets, 1995). It exhibits the craniocaudal expansion of the proximal end characteristic of *Phalacrocorax*. On the basis of size, it should be considered *P. carbo*. Of the two specimens placed in *fuscescens*, F3769 agrees with *varius* on size while F3768 falls into the *varius*–*fuscescens* overlap zone. Although the latter cannot be confirmed with confidence, it is here considered to be more likely a small individual of *varius*.

vetustus—The two largely complete specimens were regarded by Rich & van Tets (1982) to be *fuscescens*. They fall into the overlap zone of size between male *fuscescens* and female *varius*. As with the specimen discussed above, these are more probably small *varius*.

Tibiotarsus (Table 6). In cranial view, the epicondylus medialis extends further beyond the medial margin in *Phalacrocorax* and the distal end of the shaft lateral to the



Figure 10. Distal end of femur (caudal view) showing differences in robustness of the trochlea fibularis between (A) *Phalacrocorax* and (B) *Anhinga*.

proximal opening of the sulcus extensorius is more expanded laterally in *Phalacrocorax*. In cranial view, the crista cnemialis medialis is directed cranially in *Phalacrocorax*, rather than craniolaterally, as in *Anhinga*.

Overall size and robustness of this element serve to distinguish the species of cormorants.

gregorii—While the three distal fragments are considered to be *varius* by Rich & van Tets (1982) and this study, the fourth specimen (F3771) is in the overlap zone between *varius* and *carbo* and cannot be placed unequivocally in either.

vetustus—The placement by Rich & van Tets (1982) of both specimens with *varius* is confirmed here on the basis of size.

Tarsometatarsus (Table 7). This element in *Anhinga* is proportionally shorter with a stouter shaft, more splayed distal end, a trochlea metatarsi III that projects further distally than trochlea metatarsi IV but not as far as trochlea metatarsi II. *Phalacrocorax varius* has a more gracile shaft than either *carbo* or *fuscescens*, even in zones of size overlap, and the raised area on the plantar surface bounded by the lineae intermusculares is narrower (broader and flatter in *carbo*).

gregorii—F3775 and F3776 were referred to *carbo* by Rich

Table 5. Femora of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *c*, complete; *p*, proximal; side: *l*, left; *r*, right; sex: *M*, male; *F*, female.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
<i>Phalacrocorax gregorii</i>					
F3764	c	l	Malkuni	<i>carbo</i>	<i>carbo</i>
F3765	c	l	Wurdamankula	<i>carbo</i>	<i>carbo</i>
F3766	c	l	Wurdamankula	<i>varius</i>	<i>varius</i>
F3767	c	l	Wurdamankula	<i>Anhinga</i> [<i>laticeps</i>]	<i>carbo</i>
F3768	p	l	Lower Cooper	<i>fuscescens</i>	<i>varius</i> F / <i>fuscescens</i> M
F3769	p	r	Malkuni	<i>fuscescens</i>	<i>varius</i>
F3770	p	l	Malkuni	<i>carbo</i>	<i>carbo</i>
<i>Phalacrocorax vetustus</i>					
F3804	c	r	Malkuni	<i>fuscescens</i>	<i>varius</i> F / <i>fuscescens</i> M
F3805	c	l	Lower Cooper	<i>fuscescens</i>	<i>varius</i> F / <i>fuscescens</i> M

Table 6. Tibiotarsi of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *p*, proximal; *d*, distal; side: *l*, left; *r*, right.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
<i>Phalacrocorax gregorii</i>					
F3771	p	r	Malkuni	<i>varius</i>	<i>carbo</i> / <i>varius</i>
F3772	d	r	Lower Cooper	<i>varius</i>	<i>varius</i>
F3773	d	l	Lower Cooper	<i>varius</i>	<i>varius</i>
F3774	d	l	Malkuni	<i>varius</i>	<i>varius</i>
<i>Phalacrocorax vetustus</i>					
F3806	p	l	Malkuni	<i>varius</i>	<i>varius</i>
F3807	p	r	Malkuni	<i>varius</i>	<i>varius</i>

& van Tets (1982) but are here regarded as *varius* on the basis of their gracility. Although he listed them in his description, De Vis thought it doubtful that two specimens (F3779 and F3780) belonged to this species. "If they do, this cormorant must have varied very much in size. The last especially has an unwontedly massive appearance." Here both are referred to *P. carbo*.

vetustus—For the only tarsometatarsus he assigned to this species, De Vis noted that "The proportions of this bone are the only means of determining its place to be in the present species" (De Vis, 1905), the length and least width being less than *P. gregorii* and *P. carbo*. Rich & van Tets (1982) referred it to *fuscescens*; however, the bone's gracility and the narrowness of the plantar area between the lineae intermusculares indicate that it should be assigned to *varius*.

Pelvis (Table 8). The crista iliaca dorsalis of *Anhinga* continues from the midline along the caudal border of the alae preacetabular ilii; in *Phalacrocorax* there is no caudal ridge, the alae merging smoothly into the acetabular region of the pelvis (Fig. 11). The synsacrum in *Anhinga* is more robust through the acetabular region, particularly ventrally, such that, in lateral view, it is visible through the acetabulum, occupying most of the space; it covers 50% of this space at most in cormorants (Fig. 12).

gregorii—De Vis placed eight pelvic fragments in *gregorii* and none in *vetustus*. There are several disagreements between Rich & van Tets (1982) and this study. Two specimens are in the overlap zone for *fuscescens* and *varius* but are likely to be the latter. One also falls into a similar

intermediate region for *carbo* and *varius*. The distance across the antitrochanters in F3786 indicates that this specimen is *varius*, not *carbo*.

Discussion and results

De Vis appears to have worked under the assumption that any fossil had to represent a different species than one living, although it could be closely related. This outlook undoubtedly contributed to his recognition of the numerous fossil taxa that have now been synonymized with modern species. Additionally, his small reference collection would have been an important factor in the case of cormorants. By having only the largest species and one smaller than all taxa in the fossil sample, many specimens could not be matched and so would appear as new. Indeed, De Vis makes many of his comparisons with *P. carbo* and explicitly cites size as a diagnostic character for several specimens.

The syntypic series of *P. gregorii* is a mixture of *P. carbo* and *P. varius*, with a very minor component of *Anhinga novaehollandiae* and a heron. A number of skeletal elements of the first two species cannot be separated except on size and, even then, there is a range of overlap between them. The range of size variation even within a species could not have been discerned with De Vis' restricted number of comparative samples.

Likewise, this was undoubtedly a confounding factor in the recognition of *P. vetustus*. For example, De Vis characterized this species as "a Cormorant of smaller size and slighter build than *P. gregorii* or *P. carbo*, about intermediate between them and *P. stictocephalus* [= *sulcirostris*]"'. This succinct circumscription provides a good characterization of

Table 7. Tarsometatarsi of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: end: *c*, complete; *p*, proximal; *s*, shaft; *d*, distal; side: *l*, left; *r*, right.

QM no.	end	side	locality	Rich & van Tets (1982)	this study
<i>Phalacrocorax gregorii</i>					
F3775	d	l	Malkuni	<i>carbo</i>	<i>varius</i>
F3776	c	r	Wurdamankula	<i>carbo</i>	<i>varius</i>
F3777	p	l	Malkuni	<i>varius</i>	<i>carbo</i>
F3778	p+s	r	Lower Cooper	<i>varius</i>	<i>varius</i>
F3779	c	l	Lower Cooper	<i>carbo</i>	<i>carbo</i>
F3780	c	r	Lower Cooper	<i>varius</i>	<i>carbo</i>
<i>Phalacrocorax vetustus</i>					
F3808	s	l	Lower Cooper	<i>fuscescens</i>	<i>varius</i>

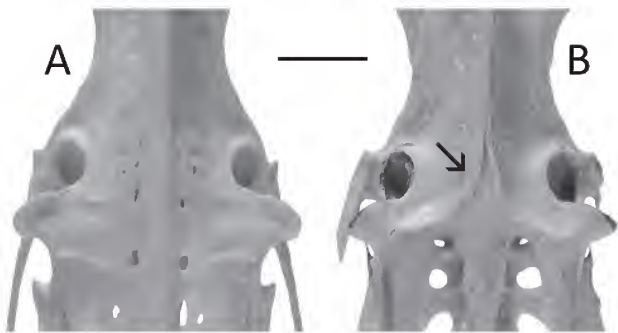


Figure 11. Pelvis (dorsal view) showing differences in development of the crista iliaca dorsalis between (A) *Phalacrocorax* and (B) *Anhinga*.

P. varius, which is smaller and more gracile than *P. carbo* but larger than *P. sulcirostris*. It is not surprisingly, then, that most of the syntypic specimens of *P. vetustus* can be referred to *P. varius*.

No incontrovertible evidence of *P. fuscescens* could be found. Almost all specimens considered by Rich & van Tets (1982) to be this species can be referred to *P. varius*. A few fall into an area of intermediacy of size or morphology and their identifications must remain inconclusive. There is no reason to invoke the presence of *fuscescens* for these in the absence of any other evidence, whereas *varius* is well represented among the remaining specimens. This also makes much more sense on distributional grounds and habitat preferences. A wide-ranging species with broad ecological tolerances is a more acceptable choice than one restricted to marine habitats along continental coasts until evidence demonstrates otherwise.

The humeral end of a coracoid (F3755) represents a large heron. Rich & van Tets (1982) correctly identified this as Ardeidae but did not make a finer taxonomic resolution. In van Tets' unpublished manuscript, he had decided that this represented the largest Australian species, *Ardea sumatrana*. This species is mangrove-specialist of the northern coast line. That such a species would be found in the waterways of central Australia during the Quaternary is most unlikely. Nonetheless, the specimen is larger than that of any other living Australian heron. It seems more probable that this might be evidence of a large, now extinct and unnamed species of heron. No specific level identification is offered here.

De Vis (1905) did not designate a holotype for either taxon. Below lectotypes are selected for *gregorii* and

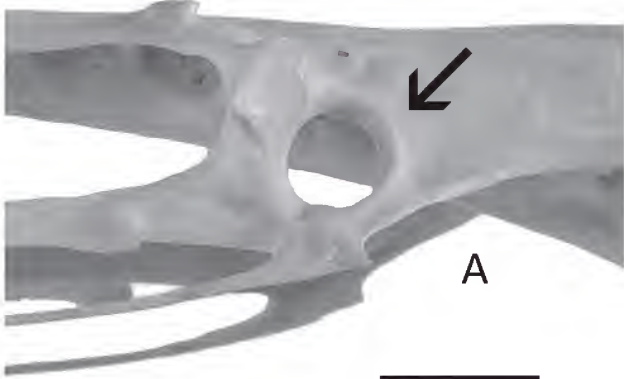


Figure 12. Pelvis (lateral view) showing differences in extent of the synsacrum visible through the acetabulum between (A) *Phalacrocorax* and (B) *Anhinga*.

vetustus, which will serve to place these putative taxa into the synonymy of living species.

The lectotype of *Phalacrocorax gregorii* is here designated to be F3756, a proximal humeral fragment, which is illustrated by De Vis (1905, plate VII, fig. 2A, B). As this has been identified as belonging to *P. carbo*, *P. gregorii* becomes a junior synonym of that species. Other specimens among the type series that are also considered here to be *carbo* become paralectotypes ([coracoid] F3754, [humerus] F3757, F3758, F3759, F3760, F3761, [carpometacarpus] F3763, F7020, [femur] F3764, F3765, F3767, F3770, [tarsometatarsus] F3777, F3779, F3780, [pelvis] F3784, F3786). The remaining fossils are either *P. varius* or *Anhinga novaehollandiae* and no longer have any

Table 8. Pelvic fragments of De Vis' cormorants, with localities and specific identifications according to Rich & van Tets (1982) and this study. Abbreviations: *s*, synsacrum; *a*, acetabulum; *2a*, both acetabula present; sex: *M*, male; *F*, female.

QM no.	portion	locality	Rich & van Tets (1982)	this study
<i>Phalacrocorax gregorii</i>				
F3781	s+2a	Lower Cooper	<i>varius</i>	<i>varius</i>
F3782	s+a	Lower Cooper	<i>varius</i>	<i>varius</i>
F3783	s+a	Lower Cooper	<i>fuscescens</i>	<i>varius</i> / <i>fuscescens</i>
F3784	a	Lower Cooper	<i>carbo</i>	<i>carbo</i>
F3785	s	Lower Cooper	<i>carbo</i>	<i>varius</i> M / <i>carbo</i> F
F3786	s+2a	Mulcani	<i>varius</i>	<i>carbo</i>
F3787	s+2a	Wurdumankula	<i>Anhinga</i>	<i>Anhinga</i>
F3788	s	Kalamurina	<i>fuscescens</i>	<i>varius</i> / <i>fuscescens</i>

nomenclatural status. The type locality for *P. gregorii* is restricted to Malkuni. The synonymization of *gregorii* with *carbo* is sensible because most of De Vis' specimens belong to the latter species and De Vis himself remarked several times on the similarity between the two.

Phalacrocorax vetustus is placed in the synonymy of *P. varius* by selecting as the lectotype F3792, a proximal humeral fragment, which is illustrated by De Vis (1905, plate VII, fig. 3A, B). The restricted type locality is also Malkuni; paralectotypes are [coracoid] F3789, F3790, F3791, [humerus] F3792, F3793, F3794, F3795, F3796, [carpometacarpus] F3800, F3803, [tibiotarsus] F3806, F3807, [tarsometatarsus] F3808. De Vis described *vetustus* as smaller and slighter than *gregorii*, which is a good characterization of *varius*.

As a result of this lectotypification, *Australocorax*, created by Lambrecht (1933) for these species (type species *Phalacrocorax gregorii*), becomes a junior synonym of *Phalacrocorax* Brisson, 1760.

Commenting on De Vis' cormorant specimens, Stirton *et al.* (1961) stated that "These materials should afford an opportunity to derive information on alterations in the distribution of the five living species of Australasian cormorant and they may contribute to our knowledge of the ecology, fresh water versus marine, of these birds". The reanalysis of these fossils indicates that two extant species were present. Both are widespread species across the continent, avoiding the drier parts of the inland, particularly in the western and southern halves where reliable water sources are absent. These cormorants still occur in the Cooper Creek and Warburton River, suggesting that the availability of open water there might not have been too different now as it was in the Late Pleistocene.

ACKNOWLEDGMENTS. The Queensland Museum Geosciences Section (S. Hocknull, K. Spring) permitted me to work on the De Vis fossils and the collection staff of the South Australian Museum (P. Horton), Museum Victoria (W. Longmore) and Australian National Wildlife Collection (R. Palmer, I. Mason) permitted me to measure comparative specimens under their care. S. Humphreys, Australian Museum Photography Department, took the photographs. U. Göhlich and T. Worthy provided valuable comments on the manuscript. The Australian Museum for provided a venue in which to work and funds to support this research.

References

- Baumel, J.J., & L.M. Witmer, 1993. Osteologia. In *Handbook of Avian Anatomy: Nomina Anatomica Avium*, 2nd edn, ed. J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge, vol. 23, pp. 45–132. Cambridge, Massachusetts: Publications of the Nuttall Ornithological Club.
- Boles, W.E., 2005. A review of the Australian fossil storks of the genus *Ciconia* (Aves: Ciconiidae), with the description of a new species. *Records of the Australian Museum* 57(2): 165–178. <http://dx.doi.org/10.3853/j.0067-1975.57.2005.1440>
- Brown, H.Y.L., 1892. Government geologists report on country in the neighbourhood of Lake Eyre. *South Australian Geological Survey*, 1892.
- Christidis, L., & W.E. Boles, 2008. *Systematics and Taxonomy of Australian Birds*. Collingwood, Victoria: CSIRO Publishing.
- Condon, H.T., 1975. *Checklist of the birds of Australia. Part 1. Non-passerines*. Melbourne: Royal Australasian Ornithologists Union.
- De Vis, C.W., 1888a. A glimpse of the post-Tertiary avifauna of Queensland. *Proceedings of the Linnean Society of New South Wales* (ser. 2) 3: 1277–1290.
- De Vis, C.W., 1888b. Australian ancestry of the Crowned Pigeon of New Guinea. *Proceedings of the Royal Society of Queensland* 5: 127–131.
- De Vis, C.W., 1889. Additions to the list of fossil birds. *Proceedings of the Royal Society of Queensland* 6: 55–58.
- De Vis, C.W., 1892. Residue of the extinct birds of Queensland as yet detected. *Proceedings of the Linnean Society of New South Wales* (ser. 2) 6: 437–456.
- De Vis, C.W., 1905. A contribution to the knowledge of the extinct avifauna of Australia. *Annals of the Queensland Museum* 6: 3–25.
- Gaff, P., 2002. *The fossil history of the family Accipitridae in Australia*. MSc thesis, Monash University, Clayton, Australia.
- Gilbert, B.M., L.D. Martin, & H.G. Savage, 1981. *Avian Osteology*. Laramie, Wyoming: published by the authors.
- Gregory, J.W., 1906. *The Dead Heart of Australia*. London: John Murray.
- Lambrecht, K., 1933. *Handbuch der Palaeornithologie*. Berlin: Gebrüder Borntraeger.
- Linnaeus, C., 1758. *Systema Naturae per Regna Tria Naturae*, 10th edn. Holmiae: Laurentii Salvii.
- Lundelius Jr, E.L., 1983. Climatic implications of late Pleistocene and Holocene faunal associations in Australia. *Alcheringa* 7: 125–149. <http://dx.doi.org/10.1080/03115518308619624>
- Mackness, B.S., & G.F. van Tets, 1995. Status of the Late Pleistocene fossil darter *Anhinga laticeps* (De Vis, 1906). *Memoirs of the Queensland Museum* 38: 611–614.
- Marchant, S., & P.J. Higgins (coordinators), 1990. *Handbook of the Birds of Australia, New Zealand and Antarctica*, vol. 1, part A. *Ratites to Petrels*. Melbourne: Oxford University Press.
- Nanson, G.C., D.M. Price, B.G. Jones, J. Maroulis, M. Coleman, H. Bowman, T.J. Cohen, T.J. Pietsch, & J.R. Larsen, 2008. Alluvial evidence for major climate and flow regime changes during the middle and late Quaternary in eastern central Australia. *Geomorphology* 101: 109–129. <http://dx.doi.org/10.1016/j.geomorph.2008.05.032>
- Olson, S.L., 1975. The fossil rails of C.W. de Vis, being mainly an extinct form of *Tribonyx mortierii* from Queensland. *Emu* 75: 49–54.
- Olson, S.L., 1977. The identity of the fossil ducks described from Australia by C.W. De Vis. *Emu* 77: 127–132.
- Ono K., 1980. Comparative osteology of three species of Japanese cormorants of the genus *Phalacrocorax* (Aves, Pelecaniformes). *Bulletin of the National Science Museum, Japan, Series C (Geology & Paleontology)* 6: 129–151.
- Owre, O.T., 1967. Adaptations for locomotion and feeding in the Anhinga and the Double-crested Cormorant. *Ornithological Monographs* 6: 138–276.
- Rich, P.V., & G.F. van Tets, 1981. The fossil pelicans of Australasia. *Records of the South Australian Museum* 18: 235–264.
- Rich, P.V., & G.F. van Tets, 1982. Fossil birds of Australia and New Guinea: their biogeographic, phylogenetic and biostratigraphic input. In *The Fossil Vertebrate Record of Australasia*, ed. P.V. Rich and E.M. Thompson, pp. 235–384. Clayton, Victoria: Monash University Offset Printing Unit.
- Rich, P.V., G.F. van Tets, & A.R. McEvey, 1982. Pleistocene records of *Falco berigora* from Australia and the identity of *Asturæus fuscillatus* De Vis (Aves: Falconidae). *Memoirs of the Queensland Museum* 20: 687–693.
- Rich, P.V., G.F. van Tets, T.H.V. Rich, & A.R. McEvey, 1987. The Pliocene and Quaternary flamingoes of Australia. *Memoirs of the Queensland Museum* 25: 207–225.

- Siegel-Causey, D., 1988. Phylogeny of the Phalacrocoracidae. *The Condor* 90: 885–905.
<http://dx.doi.org/10.2307/1368846>
- Steadman, D.W., 1980. A review of the osteology and paleontology of turkeys (Aves: Meleagridinae). *Contributions in Science, Natural History Museum of Los Angeles County* 330: 131–207.
- Stirton, R.A., R.H. Tedford, & A.H. Miller, 1961. Cenozoic stratigraphy and vertebrate paleontology of the Tirari Desert, South Australia. *Records of the South Australian Museum* 14: 19–61.
- Tedford, R.H., & R.T. Wells, 1990. Pleistocene deposits and fossil vertebrates from the “Dead Heart of Australia”. *Memoirs of the Queensland Museum* 28: 263–284.
- Tedford, R.H., D. Williams, & R.T. Wells, 1986. Late Cainozoic sediments and fossil vertebrates. In *The Lake Eyre Basin—Cainozoic Sediments, Fossil Vertebrates and Plants, Landforms, Silcretes and Climatic Implications*, ed. R.A. Callen, J.D. Dulhunty, R.T. Lange, M. Plane, R.H. Tedford, R.T. Wells, and D.L.G. Williams, pp. 42–72, Australasian Sedimentologists Group Field Guide Series no. 4. Geological Society of Australia.
- van Tets, G.F., 1974. A revision of the fossil Megapodiidae (Aves), including a description of a new species of *Progura* de Vis. *Transactions of the Royal Society of South Australia* 98: 213–224.
- van Tets, G.F., 1984. A checklist of extinct fossil Australasian birds. In *Vertebrate Zoogeography and Evolution in Australasia*, ed. M. Archer and G. Clayton, pp. 469–475. Carlisle: Hesperian Press.
- van Tets, G.F., & P.V. Rich, 1980. A review of the De Vis fossil pigeons of Australia. *Memoirs of the Queensland Museum* 20: 89–93.
- van Tets, G.F., & P.V. Rich, 1990. An evaluation of De Vis' fossil birds. *Memoirs of the Queensland Museum* 28: 165–168.
- Woodburne, M.O., R.H. Tedford, M. Archer, W.D. Turnbull, M.D. Plane, & E.L. Lundelius, 1985. Biochronology of the continental mammal record of Australia and New Guinea. *Special Publication of the South Australian Department of Mines and Energy* 5: 347–363.